

# Phylogenetic Relationships of Platanistoid River Dolphins (Odontoceti, Cetacea): Assessing the Significance of Fossil Taxa

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**ABSTRACT.**—The superfamily Platanistoidea (*sensu* Simpson 1945) includes four extant monotypic genera of mostly freshwater dolphins (*Inia geoffrensis*, *Pontoporia blainvilliei*, *Lipotes vexillifer*, and *Platanista gangetica*) and approximately 20 fossil species. Character states diagnosing the Platanistoidea are almost entirely primitive, thus uninformative in revealing phylogenetic relationships. Recent phylogenetic analyses question the monophyly of the group and suggest that some of the taxa are more closely related to members of the Delphinioidea (i.e., extant and fossil dolphins, porpoises, narwhals, and belugas). Studies of soft-anatomical characters, including nasal passage anatomy and facial musculature, have elucidated relationships within the extant Odontoceti but have not resolved the status of the Platanistoidea. Although soft-anatomical characters often cannot be inferred from fossils, fossil taxa improve resolution, especially within the Platanistoidea, for the following reasons: morphological diversity seen in these fossils provides insight into the variability and distribution of some osteological characters, some fossil families (e.g., the Squalodontidae and Eurhinodelphidae) have been proposed as the nearest relatives of at least some of the extant Platanistoidea, and some of these fossil taxa represent groups temporally close to the ancestral node, allowing more accurate resolution of the ancestral condition at the internal nodes of the cladogram. If these fossil families are closely related to the Platanistoidea, their exclusion from phylogenetic studies could lead to incorrect polarity assessment, incomplete views of character evolution, and specious conclusions of relationships. Fossil taxa sometimes have been used, however, when their monophyly or phylogenetic position within the Odontoceti were in question. Recognizing nonmonophyletic groups may effectively exclude taxa from the analysis, again decreasing the probability of recovering the true phylogeny. The best inference of phylogenetic relationships will ultimately come from consideration of all available data, including fossil taxa, molecular data, and soft-anatomical characters, analyzed with rigorous phylogenetic methods.

## INTRODUCTION

Platanistoid (*sensu* Simpson 1945) river dolphins include four extant monotypic genera of mostly freshwater dolphins found only in the Amazon (*Inia geoffrensis*), Yangtze (*Lipotes vexillifer*), and Ganges and Indus (*Platanista gangetica*) river systems and a restricted area of the southwest Atlantic Ocean (*Pontoporia blainvilliei*). Additionally, approximately 20 fossil species, excluding fragmentary material, have been regarded as closely related to river dolphins (Muizon 1987:13, 1988a:162). Currently, the river dolphins are among the most endangered of all cetaceans (Brownell et al. 1989), yet their basic biology, including their systematic relationships, remains poorly known.

The taxonomy of the river dolphins has fluctuated for more than 100 years. Some researchers (Flower 1867; Winge 1921; Slijper 1936; Simpson 1945) have proposed a monophyletic origin for river dolphins, placing the genera either into one family, the Platanistidae, or into separate families within the same superfamily, the Platanistoidea, the latter arrangement emphasizing their great morphological differences. Others (Gray 1863, 1866; Miller 1918, 1923; Kellogg 1928) have regarded the extant river dolphins as polyphyletic, generally placing *Pontoporia* within the Delphinidae. During the second half of this century the river dolphins' monophyly has been widely accepted (Hershkovitz 1966; Kasuya 1973; Pilleri et al. 1982; Zhou 1982; Barnes 1985; Barnes et al. 1985; Gaskin 1985; for opposing views see Rice 1977; Fordyce 1983), despite the characters diagnosing the group, such as a long, narrow rostrum and elongate mandibular symphysis, being demonstrably primitive or equivocal at the level of the Platanistoidea. Thus the monophyly of river dolphins has not been established on the basis of shared derived features. Recent phylogenetic analyses question it (Muizon 1984, 1987, 1988a, 1991; Heyning 1989) and suggest that some genera are more closely related to members of the Delphinioidea, which include the dolphins, porpoises, narwhals and belugas. Yet none of these analyses has attempted to incorporate all available data (i.e., some analyses have not included fossils as terminal taxa, while others have excluded soft-anatomical characters).

Both Heyning (1989) and Muizon (1984, 1987, 1988a, 1991) have attempted to reconstruct the phylogenetic relationships of odontocete whales by using cladistic methodology, yet each used quite different approaches. Heyning (1989) analyzed the relationships of extant families of odontocetes by using a large number of soft-tissue characters, while Muizon (1984, 1987, 1988a, 1991), using osteological characters, focused on fossil taxa. These studies have resolved some odontocete relationships, but some of their hypotheses conflict. It is not my objective in this paper to compare these hypotheses to detect the effects of fossil taxa in phylogenetic studies, as the studies differ not only in the inclusion or exclusion of fossils but also in the choice of characters included, method of polarity assessment, and use of computer-assisted programs to generate most parsimonious trees. These studies simply represent the current state of knowledge of the relationships of odontocete whales, within the context of which I investigate the effect of the exclusion of fossils in resolving river dolphin relationships.

I have taken data on fossil taxa from Muizon (1984, 1987, 1988a, 1991), although his inclusion of nonmonophyletic fossil taxa and use of fossil taxa with unresolved relationships may undermine his hypotheses, as will be seen below.

## PREVIOUS CLADISTIC STUDIES

With the addition of fossil taxa into a phylogenetic analysis of the Odontoceti, Muizon (1984) concluded that the river dolphins are paraphyletic (i.e., not including all of the descendants of their most recent common ancestor). The fossil families included in his studies, such as the Squalodontidae, Squalodelphidae, and Eurhinodelphidae, are important in their being more diverse osteologically than any extant odontocete family. When included in an analysis with extant odontocetes, their unique combination of primitive and derived character states introduced a greater degree of character conflict and imposed topological changes in the phylogenetic hypotheses. Among the extant river dolphins, Muizon (1988a, 1991) retained only *Platanista* in the Platanistoidea (Fig. 1a, Platanistidae). He placed *Pontoporia* and *Inia* in the Iniioidea, the sister taxon to the Delphinioidea, *Lipotes* in the Lipotoidea, the sister taxon to the clade including both the Iniioidea and Delphinioidea.

Soft-tissue characters of the nasal passage complex, used by

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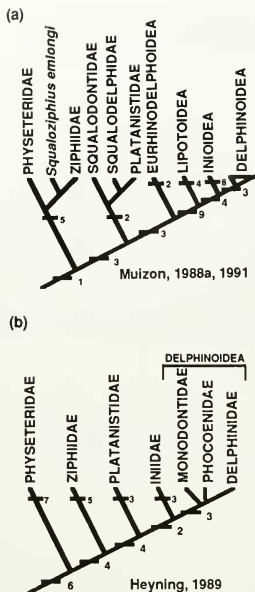


Figure 1. Alternative hypotheses of relationships of the Odontoceti. (a) Cladogram based on both extant and fossil taxa, redrawn from Muizon (1988a, 1991). The Iniioidea include *Pontoporia* and *Inia*. (b) Cladogram based on 42 (including 18 soft-anatomical) characters of extant taxa only (from Heyning 1989). The Iniidae include *Inia*, *Lipotes*, and *Pontoporia*. Numbers next to bars indicate the number of synapomorphies supporting that clade.

Heyning (1989) in his analysis of extant odontocetes, also has resolved some relationships among extant odontocete families (Fig 1b). For example, Heyning (1989) cited the development of a vestibular sac as one of the synapomorphies (i.e., shared, derived character states) linking the Iniidae (including *Inia*, *Pontoporia*, and *Lipotes*) with the Delphinoidea to the exclusion of *Platanista*, also implying that the Platanistoidea (*sensu* Simpson 1945) are paraphyletic or polyphyletic. He did not address relationships within the Iniidae. Although both studies concluded that platanistoids are not monophyletic and separated *Platanista* from the remaining river dolphins, Heyning (1989) did recognize the other three river dolphins as a monophyletic taxon, the Iniidae, whereas Muizon (1988a) indicated that this grouping is itself paraphyletic. Nonetheless, Heyning (1989) stated that platanistoid relationships have not been resolved conclusively and emphasized the need for all platanistoid species to be reanalyzed.

Another and perhaps more significant difference in the two proposed hypotheses is in the relationship of ziphiids to physeterids. Four characters of the nasal passage (confluence of nasal passages,

presence of a blowhole ligament, presence of premaxillary sacs, and development of the proximal sac into an inferior vestibule/nasofrontal sac/posterior nasal sac complex) were used by Heyning (1989) as synapomorphies uniting the Ziphiidae (beaked whales) with the clade including the Platanistidae (*Platanista* only), Iniidae, and Delphinoidea and excluding the Physeteridae. Soft-anatomical features were also among the character states he used to unite *Physeter* and *Kogia* into a monophyletic group, the Physeteridae (presence of a spermaceti organ and frontal and distal sacs), and to establish the monophyly of the Ziphiidae (presence of throat grooves). Yet Muizon (1984, 1991) recognized the Physeteridae and Ziphiidae as a monophyletic group. On the basis of features evident in fossil taxa, especially *Squaloziphius emlongi*, which he considered a ziphiid, Muizon (1984, 1991) determined that characters previously thought to be primitive for odontocetes, such as the absence of the lateral plates of the pterygoids, were derived in parallel in the clade including physeterids and ziphiids and the clade including the remaining odontocetes.

These examples demonstrate the need for a re-evaluation of the Platanistoidea, as well as odontocetes in general. Although neither soft-anatomical characters nor fossils resolved platanistoid relationships, the value of both has been clearly demonstrated.

#### EFFECTS OF EXCLUDING TAXA ON PHYLOGENY RECONSTRUCTION

Many have debated the usefulness of fossil taxa in phylogenetic analyses (Simpson 1961; Hennig 1966; Patterson 1981; Doyle and Donoghue 1987; Gauthier et al. 1988; Donoghue et al. 1989; Huelsenbeck 1991; Novacek 1992). While some (e.g., Simpson 1961) have advocated the special qualities of fossils, emphasizing ancestor-descendant relationships, others (e.g., Patterson 1981) have contended that fossils offer no additional information and should not affect the topology of a cladogram based solely on extant taxa. Yet Doyle and Donoghue (1987), in their phylogenetic analysis of angiosperms, and Gauthier et al. (1988), in their re-evaluation of amniote relationships, have demonstrated that the consideration of fossil taxa can affect hypothesized relationships dramatically. Huelsenbeck (1991), through the use of computer simulations, has proposed conditions under which fossils might provide both more and less resolution than extant taxa alone. According to Gauthier et al. (1988), "fossils should be most important in phylogenetic inference when the group of interest is old and only a few, highly modified, terminal taxa are extant." This statement agrees with Felsenstein's (1978) prediction that parsimony methods can be positively misleading (i.e., the method will not converge on the real phylogeny despite the addition of more data) in lineages in which the scaled lengths of branches leading to terminal taxa are much longer than those of internal branches. This situation is directly applicable to the river dolphins. Each of the four monotypic extant genera exhibits a unique combination of primitive and derived character states. In my own analyses, I have found for the river dolphins many more autapomorphies than characters elucidating relationships among them. These four extant species constitute less than 20% of the total number of known river dolphin species, even if only well-preserved fossil taxa are considered. Also, several families within the river-dolphin group, as defined by Muizon (1984) (e.g., Squalodontidae, Squalodelphidae), as well as in cetaceans in general [e.g., Archaeoceti, Eurhinodelphidae (= Rhabdocetidae), Cetotheriidae], are represented exclusively by fossil members, evidence that cetacean history conceals far more diversity than the order shows today. This lost diversity represents lost information.

Fossil taxa are important in systematics for the following reasons: first, fossil taxa may represent outgroups (i.e., taxa closely

related to the group under study that are used to determine the direction of character evolution) phylogenetically closer to the ingroup than are extant forms. Similarly, fossil taxa, especially those temporally close to the ancestor, should be more representative of the condition at the ancestral node. If condition at the nodes are better known, the resulting phylogeny will better approximate the true phylogeny (Huelsenbeck 1991). Second, fossil taxa may provide information on intermediate character states, showing that some characters vary continuously, although they appear discontinuous in extant taxa. Without these fossil taxa such character states may be mistakenly interpreted as nonhomologous. Third, a fossil taxon that is a sister taxon of a living form may retain many plesiomorphic character states and may render alternative hypotheses of relationships more parsimonious (Doyle and Donoghue 1987; Gauthier et al. 1988; Donoghue et al. 1989). Potential problems resulting from the exclusion of fossil taxa can be illustrated by examples in platanistoid systematics.

#### Fossils as Outgroup Taxa

Outgroup taxa are used in phylogenetic analyses to determine the direction of character transformations, i.e., polarity of character states. If fossil taxa represent outgroups phylogenetically closer to the ingroup than any extant taxon, addition of these fossil taxa could change polarity assignments at the outgroup node. Because previous investigators have proposed that some river dolphins are more closely related to members of the Delphinoidea, the ingroup in investigations of the relationships of extant platanistoids must include the Delphinoidea. Therefore, the first outgroup should be the Ziphiidae, followed by the Physteriidae and, if necessary, the Mysticeti and terrestrial mammals (Heyning 1989). In Muizon's (1984, 1987, 1988a, 1991) studies including fossil taxa, the Agorophiidae (*sensu* Fordyce 1981), Squalodontidae, Squalodelphidae, and Eurhinodelphidae represent fossil groups more closely related to the ingroup than are some of the extant outgroups. The effect that these additional fossils can have on polarity assessment is illustrated by a particularly interesting and complex structure in cetaceans, the pterygoid bone.

Cetaceans possess a pterygoid that, in some members, is divided into medial and lateral lamina (Fig. 2). The condition of the lateral lamina of the pterygoid, extending posteriorly beyond the level of the pterygoid hamulus, varies widely in the Odontoceti, especially among some of the extant river dolphins, and homologues are unclear (Cozzuol 1989a). For this example, however, I will assume that all lateral lamina are homologous. The presence of the lateral lamina of the pterygoid has been interpreted as both plesiomorphic (Fraser and Purves 1960; Muizon 1984; Fordyce 1985) and apomorphic (Barnes 1985; Cozzuol 1989a). This character can be polarized differently depending on whether or not fossil taxa are considered (Figs. 3a, b). Among extant taxa, the lateral plate is present in mysticetes (Fraser and Purves 1960), *Platanista gangetica*, *Pontoporia blainvilliei*, some species of the Phocoenidae (e.g., *Phocoenoides dalli*), and some individuals of *Lagenorhynchus albirostris* (Cozzuol 1989a). The pterygoids of the earliest-diverging extant odontocetes, the Physteriidae and Ziphiidae, lack a lateral lamina. The lateral lamina of mysticetes, creating a shallow fossa in the posterior margin of the pterygoid (Fraser and Purves 1960), differs greatly from that of any extant odontocete and may not be homologous. Therefore, by the outgroup method of Maddison et al. (1984), the lateral lamina of extant odontocetes is derived (Fig. 3a). Among fossil taxa, the pterygoid bears a lateral lamina in archaeocetes, agorophiids, ziphiids (*Squaloziphius emlongi*), squalodontids, squalodelphids, platanistids (*Zarhachis* and *Pomatodelphis*), and eurhinodelphids. If the structures are homologous and some of the fossil taxa are more closely related to the ingroup than to any extant outgroup taxon, as Muizon (1991) has

suggested, the fossil taxa imply that the lateral lamina of the pterygoid could be primitive in the clade including the river dolphins and Delphinoidea (Fig. 3b).

Similarly, the size of the posterior process of the tympanic bulla is a character whose polarity can be interpreted differently when fossil taxa are included in or excluded from phylogenetic analysis. The tympanics of the Physteriidae and Ziphiidae (and Mysticeti) exhibit a large posterior process that becomes incorporated into the cranium between the squamosal and the occipital suture and is visible on the exterior of the skull. All other extant odontocetes except *Platanista* exhibit a much smaller posterior process that is no longer visible on the exterior of the cranium; *Platanista* has a posterior process somewhat intermediate in size. Outgroup comparison of extant taxa only implies that the large posterior process of the tympanic of physteriids, ziphiids, and mysticetes is primitive and the small posterior process is derived. Muizon (1984), however, found that the posterior process of *Platanista* resembles that of agorophiids and considered this moderately small posterior process as the plesiomorphic condition in odontocetes. Therefore, he considered the enlarged posterior process of physteriids and ziphiids derived, constituting a synapomorphy uniting the two families and and their fossil relatives into a monophyletic group. He considered the much smaller process of the Lipotoidea, Inioidae, and Delphinoidea to be a derived condition representing a synapomorphy of that clade.

A character traditionally used to unite the river dolphins is their elongated mandibular symphysis. Indeed, all of them possess a mandibular symphysis measuring over one-half of the total length of the mandible. Heyning (1989), however, found that agorophiids, eurhinodelphids, and *Steno* (a delphinid) also possess elongated mandibular symphyses. Because the origin and taxonomic distribution of an elongated mandibular symphysis was unclear, Heyning gave it less weight, though he considered this character derived, having evolved independently three times, in Physteriidae, Platanistidae, and Iniidae. If the relationships of fossil and extant odontocetes proposed by Muizon (1988a, 1991) are correct and the elongated mandibular symphysis is derived, the character must have evolved independently seven times, in agorophiids, physteriids, eurhinodelphids, platanistids, *Lipotes*, iniids, and *Steno*. If the elongated symphysis is primitive for toothed whales, however, its independent loss in *Kogia*, ziphiids, and delphinoids and reappearance in *Steno* requires only five steps. With the addition of fossil taxa it is no longer more parsimonious to use the presence of an elongated mandibular symphysis to unite any of the river dolphin species.

#### Fossil Taxa and Increased Diversity of Character States

Fossil taxa can also affect phylogenetic inferences because additional information on intermediate states of characters seen in some fossils may be used to link taxa that had not been considered closely related. Extant taxa may be highly derived, with homologous features lost or difficult to detect. Fossil taxa may illustrate the variability of some characters, aiding in determining their homologies. For example, *Platanista* and its fossil relatives exhibit an articular process on the periosteal bone. This process is associated with a fossa in the squamosal bone and, in some taxa (e.g., the Platanistidae), fits so tightly into the fossa that the periosteal cannot be removed without breaking the process. A similar process seen in another fossil family, the Eurhinodelphidae, appears to be homologous. *Zarhachis*, a fossil platanistid, however, exhibits both the articular process and the process seen in the Eurhinodelphidae, indicating that these processes may not be homologous (Muizon 1987).

Some fossil taxa, such as the Squalodontidae, exhibit intermediate or additional character states not seen in any extant taxon. Two

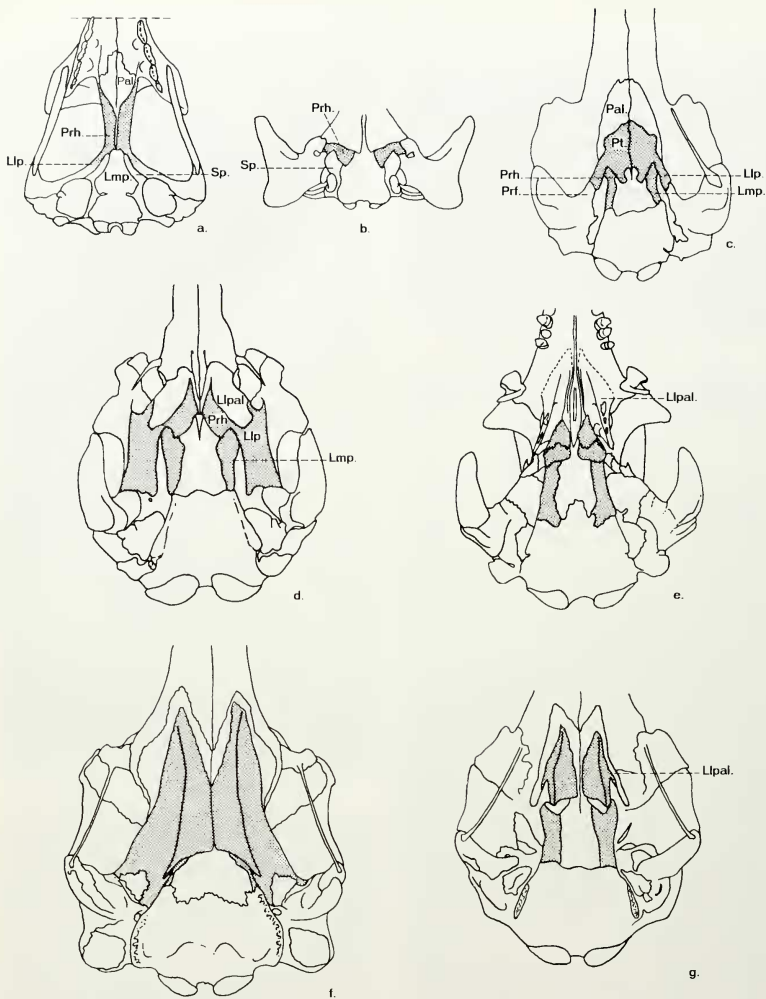


Figure 2. Ventral view of skulls showing different morphologies of the pterygoid and palatine bones in several species of cetaceans (modified from Muizon 1984). (a), Archaeocete (*Zygorhiza kochii*); (b), mysticete (*Balaenoptera musculus*); (c), eurhinodelphid (*Eurhinodelphis bossi*); (d), *Pontoporia blainvillei*; (e), *Inia geoffrensis*; (f), ziphiid (*Mesoplodon bidens*); (g), delphinid (*Lissodelphis peroni*). Llp, lateral lamina of the pterygoid; Llpal, lateral lamina of the palatine; Lmp, medial lamina of the pterygoid; Pal, palatine; Prf, falciform process; Prh, hamular process; Pt, pterygoid process; Sp, pterygoid sinus.

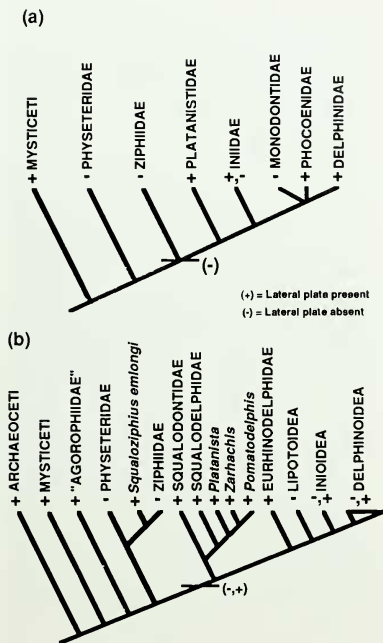


Figure 3. Distribution of states (in parentheses) of the lateral plate of the pterygoid in representative cetaceans. +, plate present; —, plate absent. (a). Cladogram based on extant taxa only (from Heyning 1989). At the outgroup node (bar) the plate is absent. (b) Cladogram based on both fossil and extant taxa (from Muizon 1991). At the outgroup node presence or absence of the plate is equivocal.

characters, a subcircular fossa in the squamosal bone and an articular process of the periotic, are unique to the Platanistoidea (*sensu* Muizon 1987, 1991). The deep subcircular fossa is positioned posteromedial to the postglenoid process of the squamosal and dorsal to the periotic. It may be a result of the expansion of the peribullary sinus, a basicranial air sinus that surrounds the periotic and tympanic bones (Muizon 1987). The articular process, discussed above, is found on the lateral surface of the periotic at the junction between the posterior process and the body of the periotic. This process articulates with a fossa in the squamosal bone at the base of the postmeatal process. These characters are well developed in *Platanista*, fossil platanistids (*Zarhachis* and *Pomatodelphis*), and the Squalodelphidae. According to Muizon (1987), they occur in some members of the Squalodontidae (e.g., *Squalodon* and *Eosqualodon*) but are much less developed. Nonetheless, these

characters have been used as synapomorphies diagnosing the Platanistoidea, as defined by Muizon (1987, 1991). In a phylogenetic analysis of extant taxa only, these characters would be considered autapomorphies of *Platanista*, thus offering no information about the phylogenetic relationships of *Platanista* within the Odontoceti. One important phylogenetic implication of this inclusion of fossil taxa (Muizon 1984, 1987) is that it is no longer most parsimonious to retain *Platanista*, with its presumed fossil relatives (*Zarhachis*, *Pomatodelphis*, Squalodelphidae, and Squalodontidae), in the clade including the remaining river dolphins.

#### Fossils as Sister Taxa Retaining Plesiomorphic Characters

Fossils may affect the topology of a cladogram if they represent sister taxa retaining plesiomorphies. As discussed above, the evidence of fossils led Muizon (1987, 1991) to unite *Platanista* with *Zarhachis*, *Pomatodelphis*, the Squalodelphidae, and Squalodontidae and separate it from the remaining river dolphins, the Inioidae and Lipotoidea. He hypothesized that the Squalodontidae and Squalodelphidae are the sister taxa of *Platanista*, *Zarhachis*, and *Pomatodelphis* (Figs. 4a, b). Muizon (1987, 1991) proposed this relationship on the basis of derived characters (e.g., subcircular fossa of the squamosal bone, articular process of the periotic), yet the Squalodontidae are otherwise primitive. To include *Platanista* and its fossil relatives in a clade with the remaining river dolphins implies a great number of reversals in the fossil taxa (Fig. 4a). For example, 12 characters of the Squalodontidae, such as heterodont dentition and unfused lacrimal and jugal bones, would have to be considered reversals. As a consequence, *Platanista*, with its fossil relatives, has been placed as the sister taxon to the clade including the Eurhinodelphidae, Lipotidae, Iniidae, and Delphinoidea (Fig. 4b). This arrangement implies that the characters shared by the platanistids, *Lipotes*, and *Inia* are convergences or plesiomorphies.

These examples illustrate that fossil taxa can indeed have a significant impact on the topology of a cladogram and should be considered in cladistic analyses.

#### ALTERNATE METHODS OF PHYLOGENETIC RECONSTRUCTION

Application of correct phylogenetic methodology (Hennig 1966; Eldredge and Cracraft 1980; Wiley 1980) is necessary to avoid erroneous inferences of relationships. Proper cladistic methodology includes the use of monophyletic groups as operational taxonomic units, polarization of characters on the basis of comparison with at least two outgroups that consist of the taxa most closely related to the ingroup (Watrouts and Wheeler 1981; Maddison et al. 1984), and the use of computer-assisted algorithms (e.g., PAUP; Swofford 1990), especially when data sets are large or characters are inconsistent. To date, only one phylogenetic study (Heyning 1989) addressing platanistoid relationships has employed a computer program (PAUP, version 2.4.1), and it did not present a published matrix of character-state assignments. Any attempt to reproduce the results of such an analysis requires that such a matrix be reconstructed on the basis of character descriptions in the text that are not always complete. Very few studies sufficiently describe character states to the species level or describe intraspecific polymorphism, both of which are necessary for accurately reconstructing character matrices. Other studies (Muizon 1984, 1987) have included nonmonophyletic taxa (e.g., the Squalodontidae) or have used alternative, less reliable methods to polarize characters, such as assuming earlier taxa are more primitive. The following examples illustrate these problems in platanistoid systematics.

A significant problem in recognizing a nonmonophyletic taxon is that some members of that taxon may be more closely related to



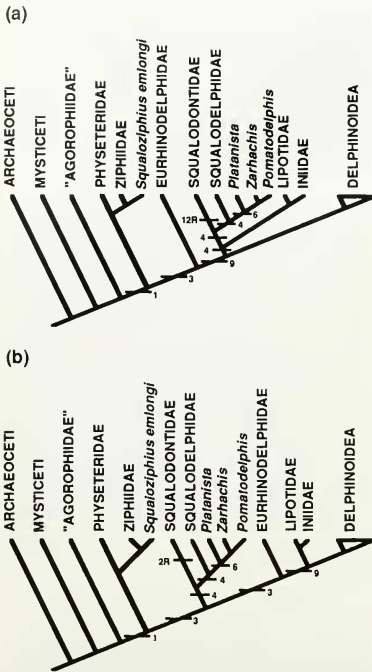


Figure 4. Alternative phylogenetic positions of *Platanista* and its fossil relatives (modified from Muizon 1988a, 1991). Muizon (1984, 1988a, 1991) has proposed that fossil taxa Squalodontidae and Squalodelphidae are most closely related to Platanistidae (*Platanista*, *Zarhachis*, and *Pomatodelphis*). Numbers, number of synapomorphies; R, reversals. (a), River dolphins constituting a monophyletic group, implying 12 reversals in the Squalodontidae. (b) It is more parsimonious to remove *Platanista* and its fossil relatives from the remaining river dolphins and place them as the sister taxon to the clade including the Eurhinodelphidae, Lipotidae, Iniidae, and Delphinoidea.

the ingroup than others. Not recognizing those members separately could have the same effect as excluding them from the analysis. Also, since a nonmonophyletic taxon can contain members of more than one monophyletic group, if the taxon is polyphyletic, such taxa may appear misleadingly diverse. As mentioned earlier, the increased diversity of character states seen in fossils can be useful in establishing homologies or uniting taxa. If these groups are nonmonophyletic, however, they could confound rather than resolve phylogenetic relationships. Alternatively, a paraphyletic taxon, by definition not including all descendants of a common ancestor, may appear misleadingly uniform. Since most phyloge-

netic studies of river dolphins (Muizon 1984, 1987, 1988a, 1991) have considered nonmonophyletic taxa, these problems need to be addressed.

Groups such as the Agorophiidae, Squalodontidae, and Eurhinodelphidae have not been demonstrated to be monophyletic but rather have been defined by plesiomorphic character states. Additionally, *Squaloziphius emlongi*, considered by Muizon (1991) to be an important early diverging ziphiid, is considered by others not to be closely related to the Ziphiidae (Heyning pers. comm.). Several of these taxa are considered by some researchers (Fordyce 1985) to be grades, and they are very possibly paraphyletic. The Agorophiidae and Squalodontidae, often described as primitive odontocetes, include stratigraphically early fossil taxa united largely by plesiomorphies such as heterodont dentition and incompletely telescoped skulls. Several of the taxa included in these families are represented by only fragmentary material. To date, no diagnosis of the Agorophiidae on the basis of derived character states has been attempted, and the group is in much need of study. Nevertheless, it has been used as an outgroup taxon in studies of platanistoid relationships (Muizon 1984, 1991; Heyning 1989).

Although Muizon (1987) stated that the Squalodontidae could be nonmonophyletic, he included that family in his redefinition of the Platanistoidae as the sister taxon of the Squalodelphidae and Platanistidae. The Squalodontidae, as defined by Winge (1921), Rice (1967), Rothausen (1968), and Barnes (1985), include the Agorophiidae. Fordyce (1985) stated not only that agorophiids did not share a most recent common ancestor with squalodontids, but also that some genera within the Squalodontidae are more closely related to other taxa, such as the Squalodelphidae and Platanistidae. Cozzou (1989b) believed the Squalodontidae to be polyphyletic and, in an attempt to resolve this problem, removed *Prosqualodon* from the family while including the eurhinodelphids. Later, Muizon (1991) proposed that a subset of the genera he had previously placed in the family (Muizon 1987) form a clade. The status of the Squalodontidae is still not completely resolved.

The monophyly of the Eurhinodelphidae is also in question and requires further study. Although Fordyce (1985) stated that this family has not been diagnosed on the basis of derived character states, Muizon (1991) listed one synapomorphy for it, lengthening of the premaxillary portion of the rostrum such that the rostrum extends farther anteriorly than the mandible. Another problematic family, the Acrodelphidae (*sensu* Abel 1905), contains species that have been placed in the Eurhinodelphidae or as the sister taxon to the Eurhinodelphidae (Muizon 1988b).

This also brings into question the monophyly of the Acrodelphidae. Barnes (1985) defined the family as including *Schizodelphis*, *Pomatodelphis*, and probably *Zarhachis* but recommended re-evaluation of it. Muizon (1988b) stated that the family had traditionally included *Acrodelphis*, *Schizodelphis*, *Eoplatanista*, *Champsodelphis*, and, according to some researchers, *Pomatodelphis* and *Zarhachis*. In his revision, he broke up the family Acrodelphidae, restricting it to the type specimen of *Acrodelphis* and leaving it as *incertae sedis*. He placed *Schizodelphis sulcatus* into the Eurhinodelphidae, stated that *Acrodelphis* is a junior synonym of *Champsodelphis*, placed *Acrodelphis ombonii* into a new genus, *Dalpiazina* [subsequently proposing it as a possible sister taxon to Squalodontidae (Muizon 1991)], placed *Champsodelphis tetragorhinus* into a new genus, *Medocinia*, included in the Squalodelphidae, and placed *Pomatodelphis* and *Zarhachis* into the Platanistidae. This example underscores the need for a re-evaluation at all levels. Under such circumstances where the taxonomy appears to be very unstable, it is best to disregard the current classification and regard each species, or specimen, as a separate operational taxonomic unit.

Not only is the monophyly of several taxa in question, so are their phylogenetic positions within the Odontoceti. This can cause

problems in determining appropriate outgroups and reconstructing character states at ancestral nodes. Some workers (Barnes 1985; Fordyce 1985; Cozzuol 1989b) have stated that at least some squalodontids represent an early-diverging lineage within the Odontoceti. At least three alternative branching sequences of the Squalodontidae have been suggested (Fig. 5): (1) as the sister taxon to the clade including the Platanistidae and Squalodelphidae (Muizon 1987, 1991); (2) as the sister taxon to the Ziphiidae (Fordyce 1985); (3) as one of the earliest diverging lineages within the Odontoceti (Barnes 1985; Cozzuol 1989b; Heyning 1989). If at least some members of the Squalodontidae are demonstrated to have diverged before the Physeteridae and/or Ziphiidae, this again could change polarity assignments for lineages branching off subsequently and ultimately may affect the topology of the cladogram.

Similarly, the Eurhinodelphidae (Fig. 6) have been suggested as (1) the sister taxon to the Delphinida (*sensu* Muizon 1988a), which include the Iniidae, Lipotidae, and Delphinoidea (Muizon 1988a); (2) an early-diverging lineage that may have originated within the Squalodontidae (Barnes 1985; Cozzuol 1989b); or (3) members of the family Delphinidae (Kellogg 1928). Fordyce (1983) mentioned similarities between eurhinodelphids and platanistids but concluded that further study is required to determine if these similarities are synapomorphies. These radically different hypotheses of relationships emphasize the need for more study of this group. Misplacement of the Eurhinodelphidae or its recognition as a nonmonophyletic family could lead to incorrect polarity assignments.

As has been demonstrated earlier, appropriate choice of the outgroups serving as the basis for character polarity is vital to inferring phylogenetic relationships. The outgroup-comparison method has been demonstrated to be the most objective method for determining character-state polarity (Watrous and Wheeler 1981). When possible, more than one outgroup should be used and the branching sequence of outgroups should be determined on the basis of shared, derived features. Yet several cladistic studies have failed to polarize character states on the basis of more than one outgroup (e.g., Barnes 1985). Others often have resorted to the stratigraphic record, generally looking at the stratigraphically earliest members of the ingroup to assign polarities (Muizon 1984, 1987, 1988a,

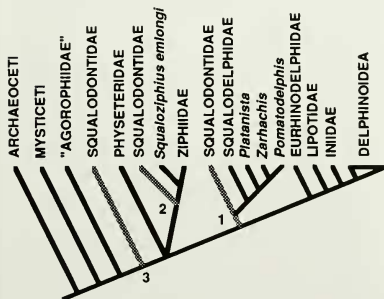


Figure 5. Alternative phylogenetic positions of the Squalodontidae, as proposed by various researchers. The family represents (1) the sister taxon of the Squalodelphidae and Platanistidae (Muizon 1987, 1991), (2) the sister taxon of the Ziphiidae (Fordyce 1985), or (3) an early-diverging lineage of odontocetes (Barnes 1985; Cozzuol 1989b; Heyning 1989).

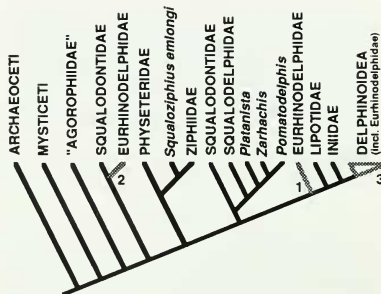


Figure 6. Alternative phylogenetic positions of the Eurhinodelphidae, as proposed by various researchers. The family represents (1) the sister taxon of the Delphinida (Muizon 1988a, 1991), (2) an early-diverging lineage originating within the Squalodontidae (Barnes 1985; Cozzuol 1989b), or (3) a subset of the Delphinidae (Kellogg 1928).

1991). When fossil taxa within the ingroup are used, characters may be polarized incorrectly and the resulting phylogenetic relationships may be based on shared primitive characters.

Finally, computer-assisted programs (e.g., PAUP, Swofford 1990) should be used to analyze phylogenetic relationships. The assumptions (e.g., whether or not characters were ordered or weighted) made during the computer analyses should be described. The matrix of character states used in the computer analysis should also be published. If character-state matrices cannot be reproduced accurately from the descriptions given in the text of a published phylogenetic analysis, the results of the analysis are not reproducible.

## DISCUSSION

Clearly, much work still needs to be done before the phylogenetic relationships of many odontocete taxa are sufficiently understood. The problems regarding the phylogenetic position and/or monophyly of some fossil taxa, however, do not negate their importance in phylogeny. As the phylogenetic relationships of the earliest diverging lineages become further resolved and monophyletic groups are identified, assessments of character polarities and hypotheses of character evolution will change. This is especially relevant for cetaceans and river dolphins in particular, of which a large proportion of the species are extinct. It is important not to attribute special qualities to fossils or to overlook the inherent biases of the fossil record. The fossil record of cetaceans is skewed, since most fossil taxa are found in deposits originating in shallow seas or estuaries and very few pelagic species are known. The selective preservation of certain bony elements, such as periotic bones or teeth, is another source of bias. Fossils inherently lack certain characters available in extant taxa, such as soft tissue and DNA. As Heyning (1989) showed, such characters also provide important information for resolution of phylogenetic relationships and should be included in data sets even though they are lacking from fossil material. Lack of certain characters is not restricted to fossil taxa. Extant taxa may be effectively incomplete if some of their characters are so highly derived that homologies cannot be determined (e.g., nasal sacs of physeterids versus other

odontocetes). The addition of fossil taxa will generally increase the number of missing characters in the data matrix. Missing character data will increase the number of equally parsimonious trees but should not give misleading trees. The increase in the number of equally parsimonious trees may be disconcerting; however, the quality of a phylogeny should not be based on its recovering a single most parsimonious tree, since that can be accomplished with relatively high reliability with randomized data, at least with molecular data (Hillis 1991; Hillis and Huelsenbeck 1992). The best approximation of phylogenetic relationships should consider all available data, including fossil taxa and soft-tissue characters, analyzed with rigorous and testable cladistic methodology.

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